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THE CAROTID CIRCULATION IN THE DOMESTIC CAT

BY

D. DWIGHT DAVIS

CURATOR, ANATOMY AND OSTEOLOGY

AND

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ASSISTANT, DIVISION OF ANATOMY



ZOOLOGICAL SERIES
FIELD MUSEUM OF NATURAL HISTORY
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CONTENTS

	PAGE
INTRODUCTION	5
CAROTID CIRCULATION IN THE ADULT CAT	7
Internal Carotid Circulation	7
The Internal Carotid Artery	8
The Ascending Pharyngeal Artery	11
The Occipital Artery	13
External Carotid Circulation	15
The Internal Maxillary Artery	15
The External Rete	17
The Orbital Artery	20
Terminal Branches of the Internal Maxillary	26
Circle of Willis	30
CAROTID CIRCULATION IN THE KITTEN AND THE FETUS	31
CAROTID CIRCULATION IN THE LION AND THE LEOPARD	33
DISCUSSION	34
Homologies with Man	35
<i>Felis</i> Compared with Other Carnivores	38
Causes for the Carotid Specializations in <i>Felis</i>	41
SUMMARY	44
REFERENCES	47



CAROTID CIRCULATION IN THE DOMESTIC CAT

BY D. DWIGHT DAVIS AND H. ELIZABETH STORY

INTRODUCTION

Comparative studies on the Carnivora being conducted at Field Museum in connection with work on the giant panda made it desirable to determine the limits of variation in the pattern of the carotid circulation within this group. Tandler's pioneer studies (1899) on the carotid circulation in the Mammalia revealed that there are extraordinary differences in this circulation within the Carnivora, but his limited material and restriction of his work to certain features of the vessel pattern were inadequate to do more than merely suggest the curious history of these vessels in the carnivores.

The cats exhibit an extreme type of carotid specialization, and our attempts to homologize their vessels on the basis of the several existing descriptions for the domestic cat were unsuccessful. In the end it became necessary to dissect a series of injected heads in order to obtain the necessary data. Our dissections revealed such gross inaccuracies and omissions in existing descriptions, particularly in Reighard and Jennings' *Anatomy of the Cat* and Hürlimann's purportedly exhaustive description, that it seems desirable to place our observations on record. Opportunity is also taken to present the relations of these vessels in a series of illustrations, which have hitherto been woefully lacking and without which any description is likely to be unintelligible. The drawings are the work of the junior author.

The material used consisted of seven latex-injected domestic cat heads from the stock of the General Biological Supply House, of Chicago. Our thanks are due that organization, especially Mr. Arnold Blaufuss, for this well-prepared material. Most of the actual dissection was carried out under a 9-power binocular microscope, which made it possible to follow the finest twigs to their destinations when necessary. Professor G. W. Bartelmez, of the University of Chicago School of Medicine, generously supplied a litter of critically important cat fetuses. The lion dissected came from the Lincoln Park Zoo, and the leopards from the Chicago Zoological Society. Dr. Harry Sicher, of the Chicago College of

Dental Surgery, has generously given valuable advice and criticism throughout the course of the study.

Norris (1906) long ago called attention to some of the inconsistencies and inaccuracies in the various descriptions of the carotid arteries in the cat. Later Hürlimann (1912) gave what was obviously intended to be the definitive description of the arteries of the head in the cat. His 72-page paper is a strange combination of painfully meticulous detail and almost incredible blunders; readily accessible vessels are usually described accurately, but most of those requiring careful manipulation must have been dissected very clumsily indeed. Hürlimann's work is further marred by the fact that he employed the confusing terminology of veterinary anatomy. No attempt was made in the latest (1935) "revision" of Reighard and Jennings to correct the extraordinary misstatements that Norris pointed out, or to utilize Hürlimann's work. We agree with Norris that Tandler's description is by far the most accurate, although it is also very incomplete for certain critical regions. Tandler's success in homologizing the vessels may probably be ascribed to the fact that he was engaged in a comparative study; experience has shown repeatedly that descriptions of blood vessels are least reliable when they are based on a single form.

Since the region under consideration is fully and adequately known only in man, and since the only rational nomenclature for mammalian anatomy is the BNA used in human anatomy, the logical procedure seemed to be to attempt a detailed homology of all the branches that have been accorded names in human anatomy. The success that attended this attempt exceeds all expectations, considering the relatively remote relation between man and the carnivores (see tables, pp. 36, 37).

We have made extensive use of our notes and dissections on other carnivores (domestic dog, various procyonids, a civet, black bear, giant panda) in evaluating and interpreting conditions in *Felis*. The literature proves abundantly that dissections of a single form, however complete and carefully made, cannot lead to trustworthy conclusions as to the history of a specialized vessel pattern. The present study amply verifies this conclusion.

Our account of the arteries is not intended to be exhaustive. Many minor muscle ramifications have not been followed out in detail, since they did not seem important in the present connection. Sufficient detail has been included, however, to provide an adequate general picture of the circulation.

CAROTID CIRCULATION IN THE ADULT CAT

The carotid trunk gives rise to three small vessels from its medial wall at the level of the thyroid cartilage, about 4 mm. behind the point where it is crossed by the hypoglossal nerve. These are the internal carotid, occipital, and ascending pharyngeal arteries (fig. 1). In seven heads (fourteen dissections) the internal carotid invariably came off first and independently, and in all but one of these seven heads a very short common trunk for the occipital and ascending pharyngeal arteries followed after an interval of a millimeter or less. In the seventh head the occipital-pharyngeal trunk was elongated to 8 mm. in length on one side, while on the other the ascending pharyngeal arose from the external carotid 11.5 mm. beyond the internal carotid. According to Tandler all three vessels arise by a common trunk, a condition not observed in any of our material but which would be expected to occur occasionally. Hürlimann, who claims to have dissected ten heads, makes the same statement as Tandler; this cannot be reconciled with our observations.

Two minute muscle twigs, one to the posterior pharyngeal constrictors and one to the sternomastoid and posterior part of the digastric, characteristically arise from the common carotid opposite the origin of the occipital-pharyngeal trunk.

The carotid body is situated at the base of the ascending pharyngeal artery. It is supplied by a twig from the occipital-pharyngeal trunk.

Beyond the origin of these small vessels the carotid trunk continues, practically undiminished in caliber, as the external carotid artery.

INTERNAL CAROTID CIRCULATION

The occipital and ascending pharyngeal arteries are so intimately related to the internal carotid circulation in the cat that it is convenient to consider these three vessels together. All branches normally arising from the proximal part of the internal carotid have been transferred to the occipital or pharyngeal arteries in the cat, obviously because of the vestigial nature of the internal carotid in this animal.

The ophthalmic artery, which is small as in other carnivores, arises from the anterior part of the circle of Willis, and hence is not directly related to the internal carotid. It accompanies the optic nerve through the optic foramen, lying to the lateral side of the nerve, and terminates in the powerful ciliary artery (p. 22). The

ophthalmic artery is often absent; it was lacking in six out of twelve cases.¹

THE INTERNAL CAROTID ARTERY²

A. carotis interna is the smallest and most posterior of the three small vessels arising at the bifurcation of the common carotid; there is a small nipple-like expansion of the common carotid at the site of its origin. It is a minute vessel, never containing any injection mass and consequently always white in color, that runs forward to the notch-like carotid foramen situated in the anterior border of the foramen lacerum posterior (fig. 1). It first crosses beneath the vagus nerve to lie immediately mesad of it, and then is situated between the internal carotid nerve (medially) and the vagus and glossopharyngeal nerves (laterally). The vessel lies between the glossopharyngeal and internal carotid nerves as it enters the carotid foramen. It crosses the roof of the medial chamber of the bulla in the carotid canal, accompanied by the internal carotid nerve (fig. 2). The artery and nerve emerge together onto the anterior part of the promontorium, where the artery bifurcates to form two feeble terminal branches. These accompany branches of the nerve onto the promontorium, where they terminate by anastomosing with terminal branches of the next part of the internal carotid, which in the cat has been transferred to the ascending pharyngeal and has reversed the direction of its flow (see p. 12). The internal carotid gives off no branches before reaching the promontorium. The distal (intracranial) part of the internal carotid has been completely taken over by the ascending pharyngeal (see p. 11).

Tandler long ago noted that the internal carotid of the cat was empty in otherwise well-injected specimens. Even latex, which has a much lower viscosity than injection masses previously in use, had failed to enter the internal carotid in any of the specimens we dissected. This led to a suspicion that this usually important artery has degenerated in the cat to a point where it is no longer perforate. Sections were accordingly made through this artery in six cats, at various levels both inside and outside the middle ear.

¹ Hürlimann's description of the ophthalmic is fantastic, with no fewer than three distinct arteries confused as parts of the ophthalmic. He does not mention the true origin of the ophthalmic from the circle of Willis and apparently failed to see it; his "roots" of the ophthalmic are actually the superior hypophyseal arteries. The second part of Hürlimann's ophthalmic actually is the internal ethmoidal, of which what appears to be the orbital part of the true ophthalmic is regarded as a branch.

² The "internal carotid" of Reighard and Jennings is the ascending pharyngeal. These authors do not mention the true internal carotid.

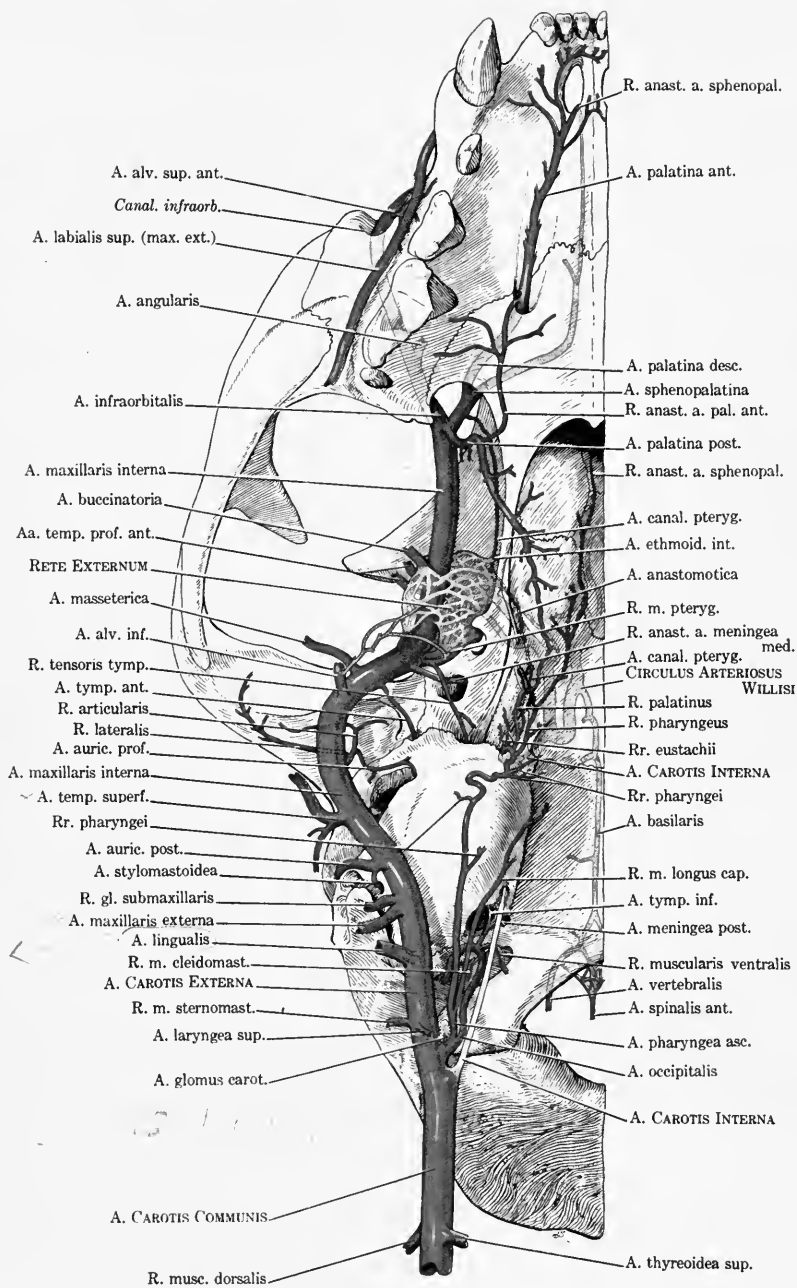


FIG. 1. Ventral view of the arteries of the head in the cat.

These reveal that the artery has a minute lumen, which was crammed with corpuscles, for a short distance beyond its origin. The walls of the vessel are immensely heavy, owing to the thickness of

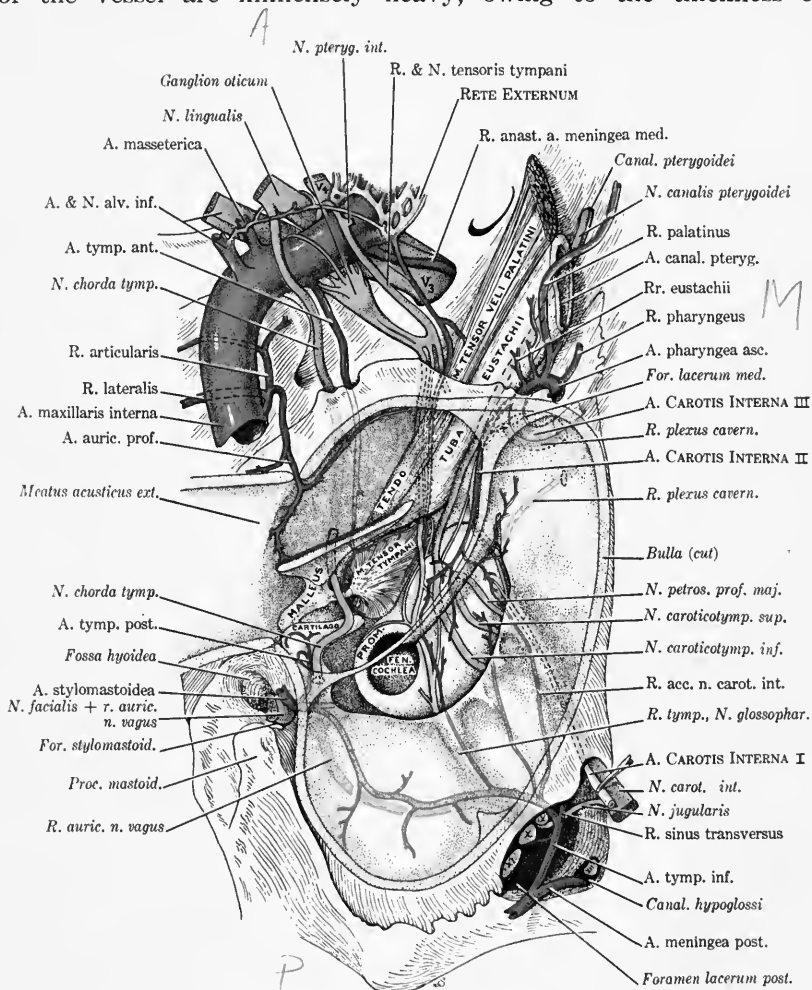


FIG. 2. Arteries of the right auditory region, seen from below. The bulla and external auditory meatus have been opened. The three divisions of the internal carotid are indicated with Roman numerals.

the tunica media; this layer is actually as thick as the media of the external carotid, although the caliber of the latter is enormously greater. Before reaching the carotid foramen the lumen disappears entirely, so that the remainder of the artery is merely an imperforate,

cordlike vestige, apparently made up chiefly of smooth muscle fibers. There is always a nipple-like reduction in the diameter of the artery just before the carotid foramen is reached. The diameter of the vessel varies in different individuals from 0.10 to 0.25 mm.

Thus in the cat the internal carotid is readily divisible into three distinct parts: (1) a posterior imperforate section, extending from the common carotid forward to the promontorium; (2) a middle section, only indirectly related to the first, extending from the promontorium to the foramen lacerum medium, which is functionally a twig of the ascending pharyngeal and in which the direction of blood flow has been reversed; and (3) an anterior (intracranial) section extending from the foramen lacerum medium to the circle of Willis, which has been taken over by the ascending pharyngeal and functionally is the direct continuation of that vessel.

Variations.—In addition to the seven cats used for dissection, the internal carotid was examined in four other specimens. In one of these eleven individuals the vessel was perforate on both sides of the head. Sections of the perforate vessel show that its wall is not thickened as in the other cats examined, although the caliber of the artery itself was small (0.20 mm.).

THE ASCENDING PHARYNGEAL ARTERY

A. pharyngea ascendens arises from the external carotid by a common trunk with the occipital artery, about a millimeter beyond the origin of the internal carotid (fig. 1). The ascending pharyngeal of the cat gives rise only to the anterior (pharyngeal and palatine) branches of the human ascending pharyngeal, the posterior (meningeal and inferior tympanic) branches coming from the occipital artery as in many other carnivores. Three to 5 mm. beyond its origin the ascending pharyngeal gives off a constant large muscle branch (*R. dorsalis* of Hürlimann) that runs anteriorly and medially to the anterior part of the longus capitis; this branch may also supply twigs to the rectus capitis and other muscles of this region.

The ascending pharyngeal pursues a somewhat tortuous course forward along the ventral surface of the bulla, situated between the bulla and the roof of the pharynx, to the foramen lacerum medium. In the cat the foramen lacerum medium is a small canal starting in the antero-medial wall of the eustachian semicanal and leading in a semicircle to its exit within the cranium at the antero-medial tip of the promontorium. The ascending pharyngeal passes through this canal into the sinus cavernosus (figs. 2, 5), to terminate in the

circle of Willis via the anastomotic artery from the external rete (p. 18), so that this part of the vessel *actually represents the distal part of the internal carotid*.

The ascending pharyngeal gives rise to the following branches (figs. 1, 2): (a) *Rr. pharyngei*, arising as it passes over the bulla, supply the anterior and middle constrictor muscles of the pharynx, the anterior end of the longus capitis (often the rectus capitis also), and the pharynx. (b) *R. palatinus* arises near the anterior end of the bulla and continues forward above the eustachian tube to the soft palate, anastomosing with the ascending palatine artery in the vicinity of the tonsil. The fine posterior division of the artery of the pterygoid canal (p. 29) opens into this artery as it crosses the eustachian tube. Just before reaching the foramen lacerum medium, the ascending pharyngeal lies against the medial wall of the eustachian tube for a short distance. Here it gives off several minute (c) *Rr. eustachii* that ramify to the eustachian tube. Immediately before entering the foramen lacerum medium, the ascending pharyngeal gives off a fair-sized twig that accompanies the eustachian tube through the eustachian semi-canal into the lateral chamber of the bulla, where it runs caudad along the septum to ramify over the promontorium. Some of its terminal twigs anastomose with the tympanic arteries on the promontorium, while others pass beneath the septum into the medial chamber of the bulla, where they anastomose with terminal twigs of the proximal part of the internal carotid. This twig is *a vestige of that section of the internal carotid that passed through the tympanic cavity*. This is shown unmistakably by comparison with the corresponding fetal circulation (fig. 8), although the reorganization involved is most extraordinary. Most striking is the complete reversal in the direction of blood flow that must take place late in fetal life; the course taken by the injection mass shows that the blood flows *from* the ascending pharyngeal onto the promontorium in the adult.

Variations.—With one exception these were limited to minor variations in the muscle branches. In six heads (twelve dissections) the typical ramifications were very constant; twigs were also supplied to the rectus capitis, digastric, jugulohyoideus, and stylohyoideus in some instances, although none of these muscles was thus supplied in more than 25 per cent of the dissections.

In one head, on one side only, the ascending pharyngeal and ascending palatine arteries anastomosed at the anterior end of the bulla, the resulting trunk entering the foramen lacerum medium.

THE OCCIPITAL ARTERY

A. occipitalis is slightly larger than the ascending pharyngeal and is situated dorsal to it. It immediately arches upward, crossing just outside the posterior cranial nerves that run back from the foramen lacerum posterior (fig. 1). There has at no time been any confusion as to the identity or main course of this vessel, although the important branches arising near its base have been consistently ignored.

Often (in about 50 per cent of the cases) a stout glandular ramus arising near its base and passing back to the large cervical lymph gland is the first branch from the occipital. In seven cases out of twelve a minute twig, arising near this glandular ramus, joined the internal carotid nerve and accompanied it onto the promontorium, where it anastomosed with terminal twigs of the second section of the internal carotid artery; in the remaining five cases this twig arose, near the foramen lacerum posterior, from the posterior branch of the inferior tympanic artery. This vessel thus duplicates the course of the posterior section of the internal carotid artery. Minute twigs to the nodose and superior cervical ganglia, and to the cranial nerves emerging from the posterior lacerated foramen, also arise from the first part of the vessel.

In the space immediately behind the posterior lacerated foramen, which is bounded laterally by the digastric muscle and medially by the ventral axial muscles, the occipital artery gives off three small vessels: (1) a muscular twig that accompanies the spinal accessory nerve to the cleidomastoid muscle and which probably represents the independent sternocleidomastoid artery of human anatomy; (2) a ventral muscle branch (*cervicalis nasalis* of Hürli-mann) to the ventral cervical muscles and the atlanto-occipital articular capsule; and (3) a vessel that bifurcates into a meningeal ramus and the inferior tympanic artery. The main trunk continues laterad across the posterior surface of the mastoid process as the occipital artery proper.

The trunk that gives rise to the meningeal and inferior tympanic arteries passes forward beside the spinal accessory nerve. It bifurcates near the hypoglossal foramen, the larger of the two resulting branches representing the posterior meningeal, the smaller the inferior tympanic (fig. 2). *A. meningea posterior* (condyloidea, Hürli-mann) enters the hypoglossal foramen, through which it reaches the posterior fossa of the skull to ramify to the dura of that fossa. *A. tympanica inferior* (not mentioned by Hürli-mann) continues

forward beside the spinal accessory nerve, to enter the skull at the antero-medial border of the foramen lacerum posterior. Just before entering the skull it divides into two branches that embrace the internal carotid nerve between them as they enter the skull. The more anterior of these branches passes into the transverse sinus, in which it runs around the posterior angle of the petrosal, to enter the periotic through a minute foramen situated about midway along its posterior border. The more posterior of the two branches accompanies the auricular branch of the vagus, crossing the floor of the transverse sinus (i.e. the roof of the bulla), to enter a minute opening in the suture between the bulla and the jugular process of the exoccipital. Continuing with the nerve laterad and anteriorly across the contact surface between the bulla and the exoccipital and mastoid process, it terminates by anastomosing with the posterior branch of the stylomastoid artery. Several twigs arising from the anterior wall of the posterior branch as it crosses the posterior part of the bulla pass forward to the promontorium, where they ramify in the mucous membrane, anastomosing with terminal twigs of the second section of the internal carotid. The largest of these twigs accompanies the tympanic branch of the glossopharyngeal nerve; a somewhat smaller twig, which accompanies the internal carotid nerve to the promontorium, usually arises from the occipital near the origin of that vessel (p. 13), but may come off here. Other twigs arising from the posterior wall of the vessel ramify over the posterior part of the dorsal surface of the bulla.

The main trunk of the occipital artery, beyond the origin of the three branches enumerated above, arches laterad across the mastoid process before ascending between the insertion tendons of the splenius and obliquus capitis anterior muscles. Several twigs pass to the foramen in the mastoid process, and irregular twigs supply the surrounding cervical muscles. At the ventral border of the complexus the artery divides into a superficial and a deep branch. The superficial branch runs between the tendons of the splenius and complexus, to terminate near the external occipital prominence by anastomosing with its fellow of the opposite side. The deep branch runs through the insertion of the rectus capitis posterior complex. Numerous twigs supply the muscles of these respective regions, and others enter the numerous foramina in the occipital bone.

Variations.—The occipital artery exhibited few important variations besides those mentioned. In one head there was a digastric twig on one side and a twig to the axial flexors on the opposite side.

EXTERNAL CAROTID CIRCULATION

In addition to the pharyngeal and occipital branches described above, the external carotid is concerned with the internal carotid circulation only via the internal maxillary artery, and therefore only that artery will be considered here. Thus four main vessels (the lingual, external maxillary, posterior auricular, and superficial temporal arteries), along with several smaller twigs, arising from the external carotid as it arches around the bulla have been omitted.

THE INTERNAL MAXILLARY ARTERY

A. maxillaris interna is the direct continuation of the external carotid beyond the origin of the superficial temporal artery, and is

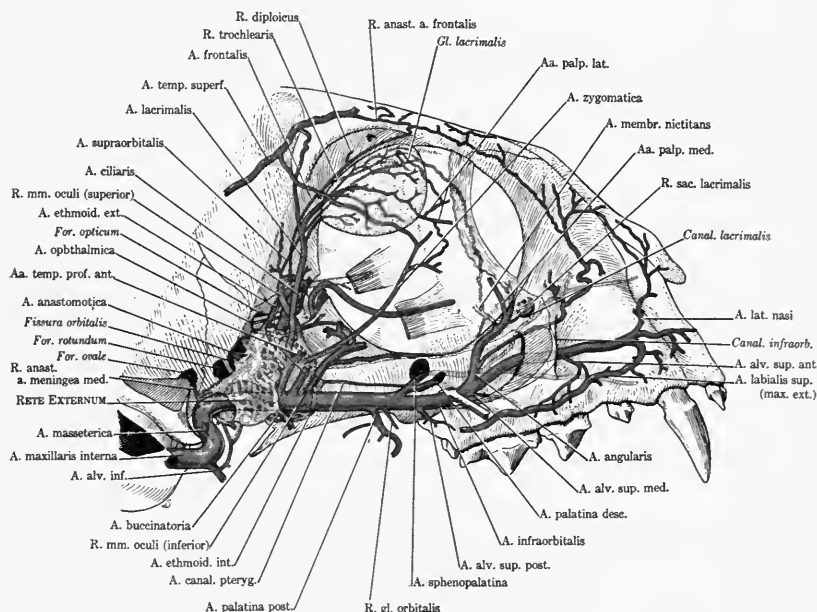


FIG. 3. Right internal maxillary artery and its branches.

by far the largest branch of the external carotid (fig. 1). It arises at the posterior border of the masseter muscle, and passes forward over the postglenoid process, then forms a sharp S-curve around the medial end of the mandibular condyle and forward into the pterygopalatine fossa. Beyond the level of the mandibular articulation it lies on the dorsal surface of the pterygoid muscles, and just anterior to the foramen ovale it is crossed dorsally by the mandibular nerve. Immediately below the foramen rotundum the artery gives

rise to the large external rete (carotid plexus of Reighard and Jennings), from which most of its branches arise (fig. 5).

The branches of the internal maxillary are:

(1) *A. auricularis profunda* (Ramus für das Mandibulargelenk, Hürlimann) arises at the anterior border of the cartilaginous meatus, and immediately bifurcates into medial and lateral branches. The *medial branch* divides again into an articular branch and an auricular branch. The articular branch, which arose independently, anterior to the auricular, in two cases out of eleven, supplies the posterior part of the capsule of the mandibular joint. The auricular branch runs mesad and dorsad in front of the meatus, dividing into two terminal twigs. One of these ramifies to the outer surface of the meatus, while the other perforates the meatus at the juncture of its bony and cartilaginous parts. The latter divides into terminal twigs upon reaching the tympanic membrane; one of these passes downward along the anterior margin of the membrane, while the other passes backward along its upper margin, terminating by following the edge of the manubrium mallei along the tympanic membrane. The *lateral branch* runs laterad across the postglenoid process. It supplies twigs to the posterior part of the mandibular capsule; its terminal twigs run forward into the coronoid fossa where they ramify to the masseter.

(2) *A. alveolaris inferior* arises at the level of the mandibular condyle, and passes dorsad of the internal pterygoid muscle to the mandibular foramen. It is situated laterad of the inferior alveolar nerve as the two enter the foramen. A twig arising from the inferior alveolar near its base supplies the pterygoid muscles by one twig, while a second twig accompanies the lingual nerve. In two cases out of eleven the inferior alveolar and masseteric arteries arose from a common base.

(3) *A. masseterica* arises opposite the inferior alveolar artery and passes up behind the coronoid process of the mandible, where it divides into a masseteric ramus and a posterior deep temporal ramus; the masseteric ramus accompanies the masseteric nerve. *R. massetericus*, which slightly exceeds the posterior deep temporal in caliber, runs outward along the anterior part of the temporo-mandibular joint, supplying a twig to the anterior part of the joint; it terminates in the masseter muscle, where it anastomoses with a masseteric twig from the external maxillary artery. *R. temporalis profundus posterior* ramifies in the lower posterior part of the temporal muscle.

(4) *A. tympanica anterior* arises from the internal maxillary opposite the masseteric artery and about 2 mm. beyond the inferior alveolar (fig. 2). It runs straight caudad to the petrotympanic fissure (in the cat this is a minute opening, usually just mesad of the canal of Hugier for the chorda tympani, in the suture between the sphenoid and the anterior border of the bulla), through which it reaches the lateral chamber of the middle ear. Here it passes back, above the tensor veli palatini, to the tensor tympani, in which it terminates, terminal twigs anastomosing with the R. tensoris tympani (p. 20). Lateral twigs from the anterior tympanic ramify to the lining of the lateral chamber. In two cases out of ten the anterior tympanic took origin from a slender anastomotic loop that connects the inferior alveolar artery with the posterior end of the external rete.

THE EXTERNAL RETE

Immediately beyond the origin of the anterior tympanic, the internal maxillary gives rise to the extensive *Rete externum* (figs. 1, 3, 4, 5). This rete is a complex network of fine vessels, interlaced with the vessels of the venous pterygoid plexus, that completely surrounds the trunk of the internal maxillary artery from the foramen rotundum to the level of the optic foramen. Thus the anterior tip of the rete extends forward inside the periorbita. The bulk of the rete lies above and mesad of the trunk of the artery. The rete also surrounds the second branch of the trigeminus, while the third trigeminal branch lies immediately external to it, one of the most posterior roots of the rete usually passing external to the inferior alveolar and lingual branches of this nerve. Fine twigs arising irregularly from the rete pass up into the temporal muscle.

Cross sections were made through the rete and examined under the microscope. These show (fig. 4) a loose plexus of small vessels, about 75 in number on a typical section, associated with the trunk of the internal maxillary artery; the entire plexus is enclosed in a thin sheath of dense connective tissue, and similar sheaths encase the nerves that pass through the rete. The vessels are fairly uniform in caliber, 0.20 to 0.30 mm. in diameter, and there are frequent interanastomoses that give the whole a sponge-like texture. Both the internal maxillary and the vessels of the rete are very thin-walled. The spaces between the vessels represent the associated venous plexus; masses of corpuscles are distributed through them, and under high magnification the venous endothelium forming the outermost layer of the arteries can be distinguished. There appears to be no

connective tissue stroma binding the arteries of the plexus together, although there is a small amount of loose connective tissue between the outermost vessels of the plexus and the sheath that encloses the whole.

The rete of the cat thus belongs to the "network" rather than to the "vascular bundle" (radiating fan) type of retia. It differs notably from any of the retia known from various parts of the body in edentates, lemurs, sirenians, and cetaceans (Wislocki and Straus, 1932; Fawcett, 1942) in the sinus-like arrangement for the venous blood and the associated absence of connective tissue stroma. As pointed out below, it is certainly a secondary development rather than a retention of the primary embryonic vascular network.

(5) *A. anastomotica* (distal rete branches of Hürlimann).—Opposite the orbital fissure the antero-medial part of the external rete gives rise to several powerful vessels that pass back through the orbital fissure into the sinus cavernosus, where they unite to form an enormous anastomotic artery that continues posteriorly in the sinus to the level of the dorsum sellae (fig. 5). Here, joined by the much smaller third section of the internal carotid (=ascending pharyngeal), the anastomotic ramus arches sharply anteriorly; at the level of the hypophysis it perforates the dura and passes into the circle of Willis, forming by far the major contribution of blood to that structure. Within the sinus collateral branches of the main anastomotic trunk form a *Rete internum* (Hürlimann's "Rete der Schädelbasis"), much smaller than the external rete, that lies against the semilunar ganglion. Numerous short twigs from the internal rete supply this ganglion. The superior and inferior hypophyseal vessels, which Wislocki (1937) described as coming from the internal carotid, actually arise from this anastomotic artery (fig. 5), although the latter is of course at least in part homologous with the internal carotid of other mammals.

The following branches arise from the trunk of the internal maxillary within the external rete, passing through the rete on the way to their destinations, or take origin from the rete itself:

(6) *A. meningeae media* is somewhat modified in the cat from its usual condition in other mammals. An anastomotic vessel arises from the trunk of the internal maxillary immediately beyond the origin of the anterior tympanic, or from the extreme posterior end of the rete itself. This vessel, corresponding in origin to the normal origin of the middle meningeal, runs through the foramen ovale into the middle fossa of the cranium, then arches mesad across the base

of the semilunar ganglion immediately below the ventral end of the tentorium. It terminates on the root of the ganglion by anastomosing with a large loop from the posterior end of the internal plexus (see below). The middle meningeal artery arises as a relatively small branch from the middle of this anastomotic vessel (fig. 5). It ramifies to the dura of the middle fossa in the usual way.

Our specimen of *Nandinia* exhibited a similar anastomotic vessel, except that its medial part (which in this animal opens directly into

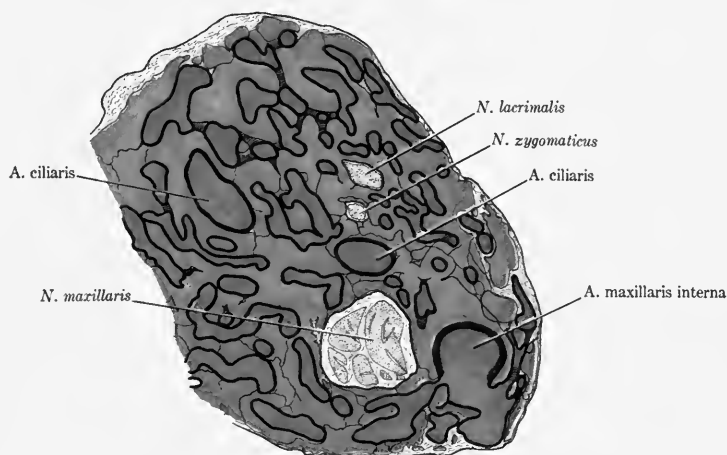


FIG. 4. Semi-diagrammatic cross section approximately through the center of the external rete, to show its sinus-like arrangement. The internal edge of the rete (to the left) has been cut because the large vessels passing into the cranium come off here. Note the absence of connective tissue except immediately beneath the sheath. Arteries are shown in red, veins in blue. Outlines drawn with camera lucida. $\times 9$.

the internal carotid) is quite subordinate to the middle meningeal so that the vessel may properly be called "middle meningeal" from its origin. From this it appears (1) that the stout anastomotic loop connecting the internal maxillary and internal carotid via the foramen ovale may characterize ailuroid carnivores, and (2) that in the cat it has increased in caliber, thus functionally taking over the origin of the middle meningeal, as a part of the general diversion of blood from the internal maxillary to the brain.

The superficial petrosal ramus and superior tympanic artery arise from the loop from the posterior end of the internal plexus mentioned above. *R. petrosus superficialis* accompanies the great superficial petrosal nerve into the facial canal, terminating by anastomosing with the stylomastoid artery. *A. tympanica superior*

enters the fissure between the tentorium (parietal) and the petrosal, immediately above the facial canal. Passing to the tympanic cavity through this fissure, it anastomoses with the other tympanic arteries. (The ganglionic twigs to the semilunar ganglion come from the internal rete; see above and fig. 5.)

(7) *Rr. pterygoidei* are several short twigs that arise from the extreme posterior part of the external rete and pass to the internal and external pterygoid muscles.

(8) *R. tensoris tympani* is a slender branch usually arising with the muscle twigs to the pterygoid muscles from the base of the rete (fig. 2); in two cases out of nine it arose from the trunk of the internal maxillary itself. The vessel joins the tensor tympani nerve and accompanies it, passing through the canalis musculotubarius above the tensor veli palatini, which it supplies, then below the eustachian tube, to the tensor tympani muscle, in which it terminates. A terminal twig anastomoses with a twig of the anterior tympanic artery.

(9) THE ORBITAL ARTERY

(Figs. 3, 5)

The orbital artery and its ramifications in carnivores correspond closely to the ophthalmic circulation of human anatomy, the only essential difference being that in man the main root, from the internal maxillary, has been given up in favor of the ophthalmic root. In the cat the various branches of the orbital artery arise independently from the internal maxillary and the anterior end of the external rete, so that no fewer than seven separate branches are involved. Since this obviously represents a secondary specialization, it seems desirable in the interest of clarity to retain the name "orbital artery" for the complex; individual names would merely mask fundamental homologies.

The ciliary, ethmoidal, deep anterior temporal, lacrimal, frontal, zygomatic, and supraorbital arteries and their branches all belong to the orbital artery circulation. They all arise in the region of the anterior part of the external rete.

(a) *A. ciliaris* (r. bulbi of Hürlimann) is the largest orbital branch of the internal maxillary, arising from its medial wall at about the level of the anterior border of the foramen rotundum. It pursues a tortuous course forward through the external rete, then perforates the external wall of the periorbita near its posterior end to enter the orbit. Within the orbit it passes between the rectus lateralis

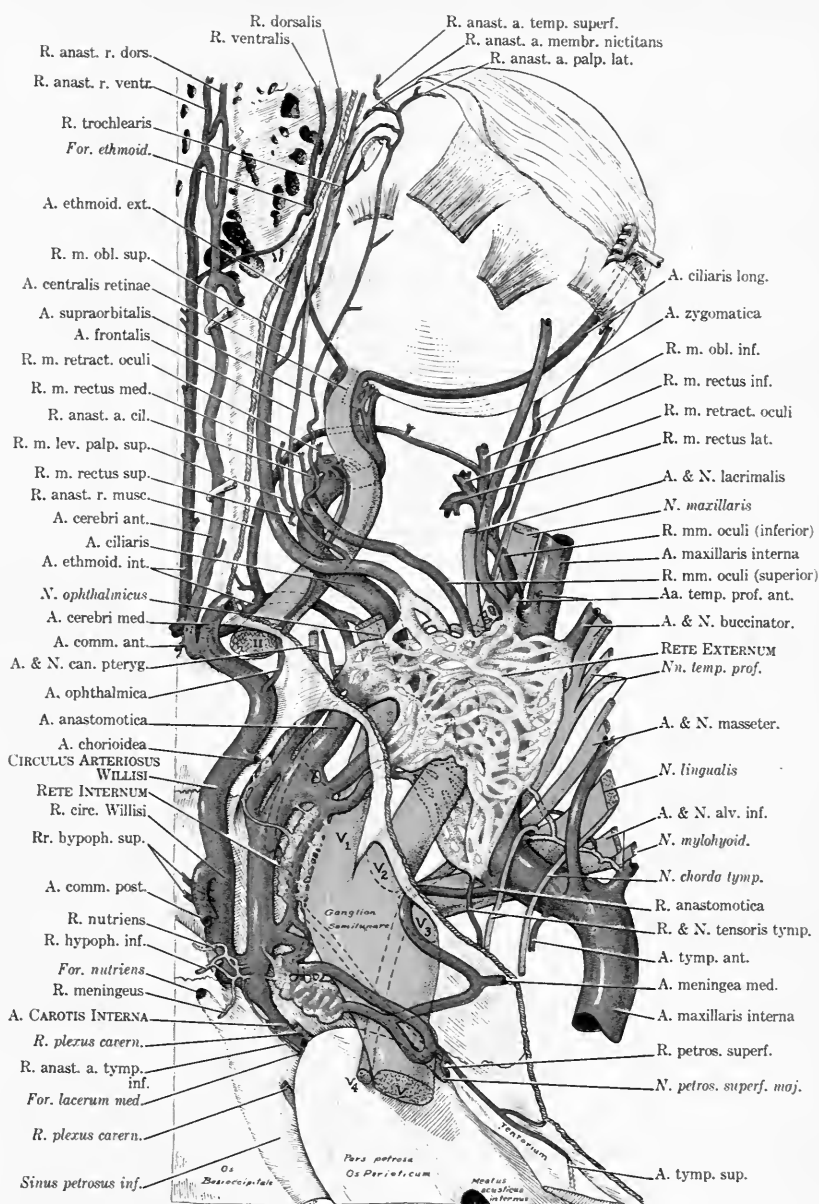


FIG. 5. Arteries of the right basicranium and orbit, viewed from above.

and rectus superior muscles, then between the parts of the retractor oculi, to reach the optic nerve. Here it is reinforced by receiving the slender ophthalmic artery and the terminal twigs of the muscular ramus that corresponds to the "superior set" of human anatomy.

In its course the artery and its terminal branches make a complete spiral revolution around the optic nerve. First crossing above the nerve to its medial side, the ciliary artery receives the ophthalmic and muscle branches mentioned above, then crosses beneath the nerve to its lateral side. Beneath and on the lateral side of the optic nerve the vessel breaks up into its numerous terminal ciliary branches, which interanastomose before entering the eyeball.

A. centralis retinae could not be located by gross dissection, even under relatively high magnification. Sections through the optic nerve revealed, however, that a fine, completely occluded vessel enters the nerve about 7 mm. behind the eyeball and continues toward the eye in the substance of the nerve. This vessel, whose lumen is obliterated by thickening of the muscular layer as is the case with the internal carotid, undoubtedly represents a vestige of the central retinal artery.

A stout branch arises from the dorsal wall of the internal maxillary beyond the origin of the ciliary artery. It may easily be traced through the external rete, from which it receives several accessory roots, and within which it divides into the lacrimal artery and one of the deep anterior temporal arteries. (b) *A. lacrimalis* accompanies the lacrimal nerve forward between the superior and lateral rectus muscles to the posterior border of the lacrimal gland, where it breaks up into its terminal branches. One or more of these ramifies exclusively to the lacrimal gland. Another runs across the gland, ramifying twigs to the gland, and terminates at the lateral corner of the eye by breaking up into numerous *Aa. palpebrales laterales*, which ramify over the conjunctiva and anastomose with the medial palpebral arteries in the eyelids. A third branch runs up to anastomose with the superficial temporal artery at the postorbital process. A diploic branch to the frontal sinus, which usually arises from the frontal artery, came from the lacrimal in two out of nine dissections.

(c) *A. temporalis profunda anterior* is represented by two or more separate vessels. One of these is always a branch of the trunk under consideration, while the others arise from the anterior part of the external rete or from the trunk of the internal maxillary. All these vessels ascend in the anterior part of the temporal muscle, which they supply.

(d) *A. zygomatica* is a slender vessel accompanying the zygomatic nerve along the inferior border of the lateral rectus and through the zygomatico-orbital canal. With the nerve it ramifies to the skin at the lateral angle of the eye, anastomosing with the superficial temporal artery. Twigs arising before the vessel passes through the zygomatico-orbital canal supply the periorbita at the lateral corner of the eye, anastomosing with twigs from the lateral palpebral arteries.

(e) *Rr. musculares* are represented partly by a constant large vessel arising from the anterior part of the external rete. It corresponds to the "inferior set" of human anatomy, running between the lateral and inferior recti and supplying those muscles, the inferior oblique, and the retractors.

A vessel arising from the anterior part of the external rete and passing between the lateral and superior recti corresponds to the "superior set" of muscle branches of human anatomy. It gives off twigs to the levator palpebrae, the superior and medial recti, and the retractors; its trunk terminates, near the terminal rete of the ciliary artery, by breaking up into numerous fine twigs that open into the ciliary artery together with the ophthalmic. The twig that supplies the levator palpebrae superioris and rectus superior constantly gives off the extremely slender *A. supraorbitalis* near its base. The supraorbital artery runs forward in the orbital fat along the medial border of the levator palpebrae to the level of the trochlea, supplying twigs to the levator palpebrae and rectus superior on the way. At the trochlea it breaks up into its terminal ramifications. One of these anastomoses with the trochlear ramus of the frontal artery, another with a muscle twig from the external ethmoidal, while several twigs interanastomose with the lateral palpebral artery and the artery to the nictitating membrane.

In one case out of nine the frontal artery took origin from the superior muscle branch.

There is considerable confusion in the literature regarding the ethmoidal arteries of carnivores. All authors have recognized an ethmoidal vessel arising from the internal maxillary and entering the cranium through the ethmoidal foramen. Mivart, Tandler, and Reighard and Jennings mention only this vessel. Others have described in addition an ethmoidal vessel that arises from the external rete and enters the cranium through the optic foramen (Norris, Hürlimann). Ellenberger and Baum (1891, *Anatomie des Hundes*) and Hofmann described a vessel with a similar course and distribution for the dog, but arising from the anterior cerebral artery

instead of entering the cranium through the optic foramen; we have found a similar condition in all carnivores examined except the cats.

Naturally the proper nomenclature for these vessels is contingent upon homology with corresponding human structures. We have carefully followed, in a dog, the course of the ethmoidal nerve and the artery that accompanies it through the ethmoidal foramen. Immediately upon emerging into the olfactory fossa, both nerve

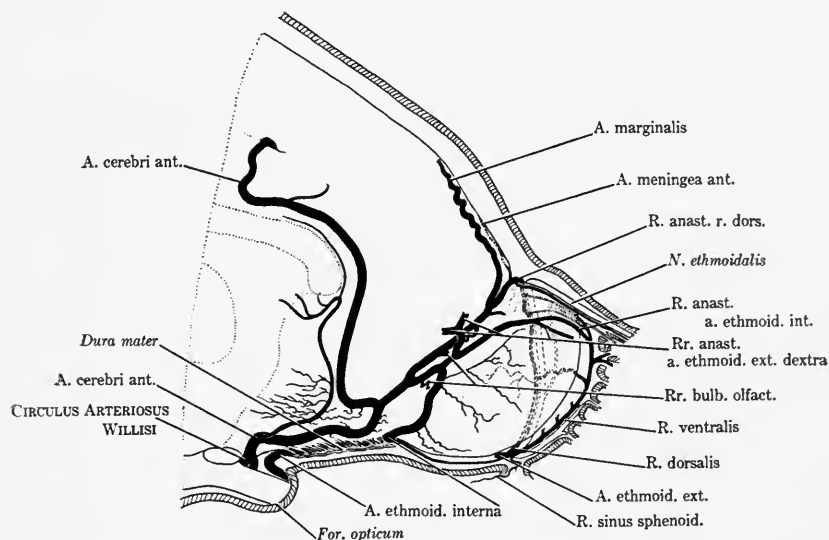


FIG. 6. Distribution of the left ethmoidal arteries. Medial view of anterior part of left forebrain.

and artery give off twigs to the ventral (posterior of human anatomy) ethmoidal cells and to the sphenoidal sinus. Hence there can be no doubt that the artery passing through the ethmoidal foramen in carnivores represents the combined anterior and posterior ethmoidal arteries of man. On the other hand, there appears to be no homologue in man for the ethmoidal artery arising from the anterior cerebral. We propose, therefore, to call the vessel passing through the ethmoidal foramen the *external ethmoidal* artery, and that arising from the anterior cerebral the *internal ethmoidal* artery (fig. 6). The origin of the internal ethmoidal from the external rete (internal maxillary) in the cat is a secondary specialization (see below).

(f) *A. ethmoidalis externa* (ophthalmica externa+ethmoidalis externa of Hürlimann) arises from the antero-dorsal part of the rete as a common trunk with the frontal artery; the trunk gives off the

frontal about 5 mm. before reaching the ethmoidal foramen, then accompanies the ethmoidal nerve forward in a groove in the medial bony wall of the orbit that leads into the ethmoidal foramen. Passing into the olfactory fossa of the cranial cavity, it immediately divides into dorsal and ventral branches. The weaker dorsal branch accompanies the main trunk of the ethmoidal nerve upward in a groove in the lateral wall of the ethmoidal fossa. It gives off numerous twigs to the ethmoidal rete and to the dura covering the olfactory lobe. The dorsal branch terminates by anastomosing with the internal ethmoidal at the postero-dorsal border of the olfactory lobe. *A. meningea anterior* is a fine twig that arises from this anastomosis and passes back into the anterior chamber of the cerebral fossa, where it ramifies. The ventral branch passes directly into the ethmoidal rete, through which its terminal twigs may be followed antero-dorsally.

Both Tandler and Norris state that the (external) ethmoidal, frontal, and lacrimal arise by a common trunk. We encountered this condition only twice, however, on both sides of one cat out of five (two out of nine dissections).

The *ethmoidal rete* is a loose network of fine vessels situated between the cribriform plate and the olfactory lobe. It is formed by interanastomosis of the terminal twigs of the external and internal ethmoidal arteries, the external making the major contribution. Numerous twigs arising from the rete pass through the cribriform plate into the nasal cavity, while others ramify over the dura covering the olfactory lobes. A fine twig from the ventral part of the rete passes into the sphenoidal sinus.

(g) *A. frontalis* is a slender trunk that accompanies the frontal nerve. Near its base it gives off an *R. trochlearis* that runs in the superior oblique muscle to the trochlea, where it anastomoses with a twig from the artery to the nictitating membrane; the trochlear ramus often arises independently from the external ethmoidal. The main trunk continues with the frontal nerve to the medial angle of the eye, where it pierces the tarsus and ramifies over the frontal area above the eye. Terminal twigs anastomose with frontal twigs from the opposite side, and with terminal twigs of the superficial temporal, angular, and supraorbital arteries.

(h) *A. ethmoidalis interna*¹ (*ophthalmica interna* [part] of Hürli-mann) arises, by two roots that soon unite, from the antero-internal

¹ In other carnivores the internal ethmoidals arise from the anterior end of the circle of Willis and pass forward along the floor of the cranium to the ethmoidal

end of the external rete and perforates the posterior part of the periorbita. Within the orbit it passes between the superior and lateral recti, then between the parts of the retractor oculi, to come to lie beneath the optic nerve. Twigs arising in this region may supply the lateral and medial recti, and a stout anastomotic branch runs forward to unite with the muscular ramus corresponding to the "inferior" set of human anatomy. Crossing beneath the optic nerve to its medial side, the vessel then passes through the optic foramen lying mesad of the nerve; an anastomotic twig to the ophthalmic artery is often given off at this point. Within the cranial cavity the internal ethmoidal fuses with its mate of the opposite side to form a common median vessel (Hürlimann's meningeal nasalis), that runs forward in the dura on the floor of the cranium. At the posterior end of the olfactory fossa it arches upward in the fissure between the olfactory lobes. Here, situated in the falx olfactorii near the posterior boundary of the olfactory lobes, it interanastomoses freely with the anterior branch of the anterior cerebral artery, while ventrally several twigs run forward to the ventral part of the ethmoidal rete. Numerous twigs are given off to the falx olfactorii, and others pierce the falx to ramify over the medial surfaces of the olfactory lobes. The vessel terminates by anastomosing with both branches of the external ethmoidal in the dorsal part of the ethmoidal rete. A much-contorted unpaired vessel, to which both the anterior branch of the anterior cerebral and the internal ethmoidal contribute, passes back above the longitudinal fissure of the cerebrum, situated in the dura over the superior sagittal sinus; this is the *A. marginalis* of Hofmann.

A strong anastomotic loop, which is usually present when the ophthalmic is absent, may pass from the anterior part of the circle of Willis to the internal ethmoidal just before the latter unites with its fellow. This condition occurred on one side only in each of two cats.

TERMINAL BRANCHES OF THE INTERNAL MAXILLARY

(Fig. 3)

Beyond the external rete the internal maxillary artery accompanies the maxillary division of the trigeminal nerve forward across

rete. Occasionally the pair of arteries unites to form a common median artery. Consequently, in all but the circulation from which it arises, the internal ethmoidal of the cat agrees with that of other carnivores, and it is of interest to note that accessory origin from the circle of Willis appears occasionally in the cat (see below). Transfer of the origin of this vessel to the internal maxillary in the cat is probably associated with the general shift of vessel origins to an extra-cranial position in the Felidae. Unfortunately it was not convenient to examine this vessel in *Nandinia*, our only civet.

the dorsal surface of the external pterygoid muscle, terminating just beyond the anterior border of the muscle by dividing into the infra-orbital and a common trunk for the descending palatine and sphenopalatine arteries. This part of the vessel gives rise to the following branches:

(10) *A. buccinatoria* arises from the ventral wall of the trunk of the internal maxillary in the anterior part of the external rete. Its origin is thus topographically associated with the origin of the separate units of the orbital artery in the cat, but it is known from the condition in other carnivores that the buccinator artery is not to be regarded as a part of the orbital artery. The vessel accompanies the buccinator nerve forward and downward to the buccinator muscle, crossing the anterior border of the coronoid process of the mandible. Good-sized twigs are supplied to the temporal and masseter muscles as the vessel crosses them, and to the orbital gland as the vessel passes beneath it. It anastomoses with the external maxillary and infraorbital arteries. No anastomosis with the transverse facial, with which this vessel also unites in man, could be found, a condition probably correlated with the reduced size of the transverse facial in carnivores.

(11) *A. palatina posterior* (palatina minor of Hürlimann) arises a short distance before the terminal bifurcation of the internal maxillary. It accompanies the nerve of the same name forward over the internal pterygoid muscle, to which it supplies twigs, to a point immediately behind the pharyngeal notch in the posterior border of the palatine. Arching backward and inward immediately behind this notch, it passes back in the substance of the palatine glands, which are situated in the soft palate between the pterygoid processes, to terminate near the posterior end of the soft palate by anastomosing with the ascending palatine artery and the palatine branch of the ascending pharyngeal. Numerous twigs to structures in the soft palate greatly reduce its caliber as it passes back. Near its origin the posterior palatine gives off a slender anastomotic ramus that runs forward over the ventral surface of the hard palate to anastomose with the anterior palatine artery.

(12) *R. glandularis*, to the orbital gland, is a small vessel or pair of vessels arising beside the posterior palatine artery. In one instance the glandular ramus came from the posterior palatine itself.

At the level of the pharyngeal notch the internal maxillary terminates by dividing into two main trunks, a lateral external

trunk distributed to structures on the side of the face, and a medial internal trunk distributed to the nose and palate.

(13) *A. infraorbitalis*, the more lateral of the two terminal trunks of the internal maxillary, accompanies the infraorbital nerve to the infraorbital foramen. Passing through this foramen onto the lateral surface of the nose, it ramifies extensively in this region. *A. alveolaris superior posterior* arises from the infraorbital near its base, and breaks up into numerous twigs that enter the foramina in the alveolar prominence over the last (fourth) premolar and first molar teeth. *A. alveolaris superior media*, somewhat larger than the posterior superior alveolar, comes off about 7 mm. behind the posterior border of the infraorbital canal and enters a foramen at the posterior border of the canal (i.e. above the third premolar). *A. angularis* (*A. malaris* of Hürlimann), which in man arises from the external maxillary, in the cat is a large vessel arising from the infraorbital artery just behind the infraorbital foramen. It passes forward immediately below the eyeball, but outside the periorbital, to the anterior (medial) corner of the eye. Here the vessel bifurcates, one twig passing above, the other below, the lacrimal sac and medial palpebral ligament. These twigs, the medial palpebral arteries, continue along the upper and lower eyelids, respectively, forming a superior and an inferior tarsal arch with the lateral palpebral arteries. Near its base the angular artery gives off a branch that passes out through the infraorbital canal, one terminal twig joining the infraorbital artery in supplying the vibrissae, while a second (*A. dorsalis nasi* of Hürlimann) runs up over the side of the nose to anastomose with the lateral nasal, frontal, and infraorbital arteries. A second branch of the angular arising about 4 mm. farther distad pierces the periorbital and runs beneath the eyeball to supply the inferior oblique and medial rectus muscles and the nictitating membrane and gland, terminating by anastomosing with the supra-orbital artery and the trochlear branch of the frontal. A third and much smaller branch of the angular, arising just before its terminal bifurcation into the medial palpebral arteries, supplies the lacrimal sac.

The main trunk of the infraorbital artery continues through the infraorbital canal onto the side of the face, where it is distributed to the upper lip, the vibrissae and the structures associated with them, and the side of the nose. It anastomoses with the superior labial artery. Numerous *Aa. alveolares superiores anteriores* enter the minute foramina over the first two premolars, the canine, and

the incisors. *A. lateralis nasi* arises from the infraorbital over the canine tooth and ramifies over the side of the nose, anastomosing with a terminal branch of the angular artery.

The more medial of the two terminal branches of the internal maxillary gives rise to three vessels. The slender artery of the pterygoid canal arises near its base, and slightly beyond this the trunk divides into the descending palatine and sphenopalatine arteries.

(14) *A. canalis pterygoidei* (fig. 1).—The artery of this name in man is represented by two separate divisions in the cat. The more anterior division is a slender anastomotic vessel extending from the common trunk of the descending palatine and sphenopalatine arteries back to the external rete. It arises at the terminal bifurcation of the trunk, then passes back successively beneath the sphenopalatine vein and the sphenopalatine ganglion, joining the nerve of the pterygoid canal at the posterior border of the ganglion and accompanying it back across the internal pterygoid muscle to the external rete, in which it terminates near the orbital fissure. The posterior division of the artery is represented by a slender vessel arising from the rete immediately behind the termination of the foregoing one. It promptly joins the nerve of the pterygoid canal, continuing with it in the pterygoid groove across the basisphenoid bone to the dorso-medial border of the eustachian tube. There the artery anastomoses with the palatine branch of the ascending pharyngeal.

The artery of the pterygoid canal is a threadlike vessel in the cat, and gives rise to no branches. The structures it supplies in man (roof of pharynx, eustachian tube, tympanum) are all supplied by the ascending pharyngeal in the cat.

(15) *A. palatina descendens* (palatina major of Hürlimann), which is smaller than the sphenopalatine artery, accompanies the anterior palatine branches of the sphenopalatine ganglion through the pharyngeal (pterygopalatine) canal, emerging on the palate through the posterior palatine foramen. Immediately upon reaching the palate, the vessel gives off a slender anastomotic branch (representing the anterior part of the minor palatine of human anatomy?) that runs back to anastomose with the posterior palatine artery.

The main trunk takes the name *A. palatina anterior* beyond the posterior palatine foramen. It runs forward on the hard palate, still accompanying the anterior palatine nerves, to the incisive (anterior palatine) foramen, where it anastomoses with the sphenopalatine artery.

(16) *A. sphenopalatina* accompanies the nasopalatine branch of the sphenopalatine ganglion. It enters the nose through the large sphenopalatine foramen, and arches up over the mucoperiosteum of the inferior nasal meatus to the nasal septum, along which it runs forward to the incisive foramen.

Immediately upon entering the nose, the sphenopalatine artery gives off a posterior lateral nasal artery to the lateral chamber of the nose. Just before reaching the nasal septum a posterior branch is given off that passes back over the roof of the nasopharynx to anastomose with the ascending pharyngeal artery. Posterior septal arteries arising as the vessel courses along the septum ramify over the septum, anastomosing with the ethmoidal arteries. The anterior terminal branches anastomose with the anterior palatine artery and the artery of the nasal septum (from the superior labial) at the incisive foramen.

CIRCLE OF WILLIS

The architecture of the circle of Willis is affected to some extent by the radical alterations in the artery patterns of the head. The circle is elongate, and is sharply divided into a powerful anterior half and a correspondingly weaker posterior half. Most of the blood is carried to the circle by the common trunk formed by the large anastomotic branches from the external carotid, which pass into the cranium via the orbital fissure; the ascending pharyngeal (= original anterior end of the internal carotid) adds a relatively small contribution to this trunk as the trunk passes the posterior border of the hypophysis, and the middle meningeal also contributes to it via the internal rete. The basilar artery, which enters the posterior end of the circle in the usual way, is also considerably weaker than the anastomotic trunk.

As it enters the circle, the anastomotic trunk divides into a posterior branch (corresponding to the *A. communicans posterior* of human anatomy) and a larger anterior branch that arches forward around the optic chiasma to divide into the middle and anterior cerebral arteries far forward in front of the chiasma. The choroid and ophthalmic arteries arise from the anterior branch before it divides into the cerebral arteries.

A. communicans anterior is extremely variable, but is not absent as stated by Hürlimann. It was not symmetrical in any one of the six brains examined (fig. 7). In only one brain was there anything resembling a typical communication between the two anterior

cerebral arteries; in this case numerous thread-like twigs to the anterior perforated substance arose directly from the anterior cerebrals. In the other five cases a large vessel arose from one anterior cerebral and passed forward in the longitudinal sulcus of the brain, supplying twigs to the olfactory areas bordering the sulcus; in two of these a minute twig arising from the opposite anterior cerebral joined the much larger vessel, thus completing the communication, but in the remaining three brains the minute twig was absent so



FIG. 7. Variations in the anterior communicating artery, showing different manners of origin of the vessel (situated between the two anterior cerebrals) that supplies the anterior perforated substance.

that there was no communication at the usual site, although fine twigs arising from both anterior cerebrals farther forward inter-anastomosed.

CAROTID CIRCULATION IN THE KITTEN AND THE FETUS

It seemed likely that occlusion of the internal carotid takes place relatively late during ontogeny in the cat, since the adult condition of the artery is reminiscent of the adult condition of the umbilical artery and ductus arteriosus in man. In an effort to verify this the internal carotid was examined in a kitten 23 days old. Sections of the vessel from this animal revealed that it was already completely occluded, and that the structure of the wall was similar to that of the adult.

On the other hand, dissection of the auditory region of fetuses measuring 80 mm. in crown-rump length supplied critical information on the morphogenesis of the carotid circulation (fig. 8). Three specimens of this litter were dissected under a binocular microscope; they yielded uniform results. The caliber of the internal carotid is more than half that of the external carotid, a relation that compares very favorably with that of "normal" carnivores. The internal carotid is perforate throughout its length, but it is extremely interesting that there is always a constriction in the vessel as it passes through the foramen lacerum posterior. After passing across the promontorium, it receives the *much smaller* ascending pharyngeal

near the anterior end of the bulla, then passes into the cranium through the foramen lacerum medium. The anastomotic ramus from the internal maxillary artery, which unites with the internal carotid as in the adult, exceeds the carotid only slightly in caliber. The

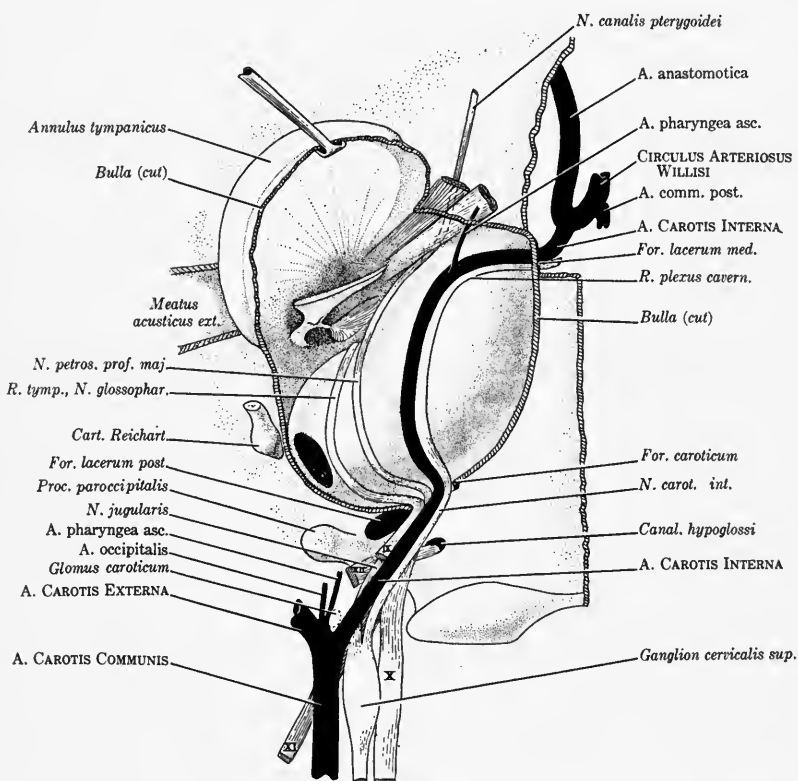


FIG. 8. Course of the right internal carotid in a fetal cat of 80 mm. C.R. length, semi-diagrammatic. The bulla has been opened and the annulus tympanicus pulled aside.

external rete is well developed, as might have been expected from Tandler's work on the pig.

The petrosal seems well ossified at this stage, but the bulla is thin, membranous, and apparently unossified; the septum bullae could not be detected by gross dissection. The bulla is also much less extensive than in the adult; nowhere does it extend beyond the periphery of the promontory. Thus the inflation that characterizes the medial chamber of the bulla in the adult must be the result of subsequent expansion, and this means that a segment of the internal

carotid between the foramen lacerum posterior and the promontorium would be squeezed between the petrosal and the dorsal wall of the expanding bulla. In the adult this part of the artery is situated in a deep groove in the bulla (entotympanic); there is no corresponding furrow in the opposing surface of the petrosal.

CAROTID CIRCULATION IN THE LION AND THE LEOPARD

The lion (*Panthera leo*) and the leopard (*Panthera pardus*), along with the other large cats, are generally regarded as quite distinct from the smaller cats of the genus *Felis*. Hence it is of interest to compare the carotid circulation of these animals with that of the domestic cat. Tandler described the carotid circulation in the tiger (*P. tigris*), leopard (*P. pardus*), and ocelot (*Felis pardalis*), but his descriptions of the vessels around the auditory region, particularly of the important relations around the foramen lacerum medium, are incomplete. We had available the heads of an adult lioness, an adult leopard, and a juvenile leopard, all from local zoos. The lion and the adult leopard at our disposal had been shot through the head, but fortunately this did not seriously interfere with complete dissection of the vessels around the bulla. The juvenile leopard was an excellent injected specimen. The general carotid pattern in these animals, as Tandler originally pointed out, is practically identical with that of the domestic cat. The internal carotid is proportionately even smaller; it measured only 0.25 to 0.30 mm. in diameter near its origin in the two adults, which is barely outside the range for the domestic cat. In spite of its minute size, however, this vessel seems to be less degenerate than in the cat. It was perforate, at least for some distance beyond its origin, in the lion and juvenile leopard, but appeared to be occluded in the adult leopard. The muscular layer (tunica media) also seems to be of normal thickness, in contrast to the cat. Tandler's description for the leopard indicates that the internal carotid was not completely occluded in his specimen; his description for the tiger is not clear for this point.

There is an extensive rete surrounding the orbital part of the internal maxillary, as in the cat,⁶ and a large anastomotic vessel passing through the orbital fissure supplies most of the blood to the circle of Willis.

The most important and consistent differences from the domestic cat are found in the auditory region, and involve the internal carotid

and ascending pharyngeal arteries. In all three specimens the internal carotid passes through the middle ear in the normal way, continuing into the cranium via the foramen lacerum medium and terminating in the anastomotic branch that supplies the circle of Willis. This contrasts sharply with the adult domestic cat, where the internal carotid is subordinated to the ascending pharyngeal beyond the foramen lacerum medium. On the other hand, it is strikingly similar to the fetal condition in the domestic cat, and is not dissimilar (except in the greatly reduced caliber of the internal carotid) to the normal carnivore condition.

The origin of the ascending pharyngeal artery differs from the domestic cat on both sides in all three specimens of *Panthera*. It takes origin independently of the occipital artery and much farther distad, beyond the origin of the lingual artery. In both the lion and the leopard the vessel runs anteriorly over the ventral surface of the bulla toward the foramen lacerum medium, but instead of the main trunk passing through the foramen and thence to the circle of Willis as it does in the domestic cat, it terminates in the usual pharyngeal branches. Only a minute, threadlike anastomotic twig passes into the foramen, where it opens into the internal carotid.

On the basis of available evidence, therefore, the carotid circulation in the larger cats of the genus *Panthera* is less specialized in the area around the bulla than in *Felis domestica*, but in general exhibits the characteristic felid stamp. Our data, added to those of Tandler, indicate that the internal carotid may be perforate more frequently than it is in *Felis*, but too few specimens have been examined to permit safe generalization on this point.

DISCUSSION

The chief objects of this study were: (a) to determine the degree to which the carotid circulation of the cat may be homologized with that of man, particularly in the interest of accurate nomenclature; (b) to determine the exact nature of the peculiar specializations to which the carnivore carotid circulation has been subjected in the cat; and (c) to determine, if possible, the cause for these specializations.

Tandler supplied the first key to this puzzle when he pointed out the important diversion of blood to the brain via the anastomotic vessel that connects the internal maxillary with the circle of Willis. Other similar but less spectacular re-routings of blood to the impoverished brain circulation have hitherto been ignored.

HOMOLOGIES WITH MAN

The accompanying table shows, more clearly than description can, the close similarity between the vessel patterns in man and the cat, a similarity that extends even to minor branches in almost every instance except where mere muscle twigs are involved. Indeed, it may be noted that differences between these two patterns involve, almost exclusively, a sort of "reshuffling" of larger trunks, with the terminal twigs affected to a much less degree or not at all.

A feature not brought out in the table, but which was repeatedly noted during this and other studies, is that interanastomoses between the terminal twigs of two or more trunks constitute one of the most constant features of a given vessel pattern. Parent trunks may wax or dwindle with variation in the number or importance of the twigs to which they give rise, as is the case with the ophthalmic artery. The trunks can shift their topographical relations with other trunks of the same system; they may interchange or recombine their terminal ramifications; and finally, two or more trunks may unite throughout all or a part of their lengths to form a common vessel, or a single vessel may break up into a number of separate entities. The terminal twigs, on the other hand, maintain a high degree of uniformity in their relations to each other and to the final structures that they supply. In general, detailed correspondence between the same vessel system in two remotely related forms (within the Mammalia) becomes increasingly close as we progress from major trunks¹ toward peripheral twigs. This fact, which is in complete accord with what is known of the ontogeny of vessel patterns, where trunks arise as local condensations in a primitive capillary plexus, does not appear to have been emphasized heretofore. Its importance from the standpoint of comparative angiology is apparent, since emphasis has hitherto been placed almost exclusively on the more individually variable main trunks. On the other hand, new pathways may sometimes be "superimposed" on the basic pattern, masking that pattern to a greater or lesser extent, as is beautifully illustrated in the carotid circulation of the domestic cat.

The carotid circulation of the cat presents three vessels not found in the corresponding circulation of man. The important anastomotic branch (p. 18) of the internal maxillary is discussed below. The orbital artery (p. 20), which corresponds closely with the human ophthalmic circulation, is of general occurrence in non-primate

¹ Exclusive, of course, of the actual conducting vessels: aorta, carotids, subclavians, iliaes, etc.

Homo

The carotid circulation in man and the domestic cat compared. The lists of vessels are not complete, only those branches of interest in the present connection having been included. The vessels are arranged in the order in which they come off, from posterior to anterior.

A. carotis communis	A. carotis interna	A. caroticotympanica [absent in <i>Felis</i>]	
		A. ophthalmica.	<ul style="list-style-type: none"> A. centralis retinae A. lacrimalis Aa. palpebrales lat. Rr. musculares A. ciliaris A. supraorbitalis A. ethmoidalis posterior A. ethmoidalis anterior A. meningea anterior Aa. palpebrales med. A. frontalis A. dorsalis nasi [absent in <i>Felis</i>]
	A. carotis externa	A. thyreoidea superior	
		A. pharyngea asc.	<ul style="list-style-type: none"> Rr. pharyngei R. palatinus Rr. eustachii A. tympanica inferior A. meningea posterior
		A. lingualis	
		A. maxillaris externa.....	(A. angularis)
		A. sternocleidomastoidea	
		A. occipitalis....	<ul style="list-style-type: none"> R. mastoideus R. auricularis Rr. musculares Rr. meningei Rr. occipitales
		A. auricularis post.	
		A. temporalis superficialis	
		A. maxillaris interna.....	<ul style="list-style-type: none"> A. auricularis profunda A. tympanica anterior A. alveolaris inferior A. meningea media A. masseterica A. temporalis prof. post. A. temporalis prof. ant. Rr. pterygoidei A. buccinatoria A. alveolaris sup. post. A. infraorbitalis.....
			<ul style="list-style-type: none"> A. alveolaris sup. ant. Rr. nasales
		A. palatina descendens	<ul style="list-style-type: none"> A. palatina major Aa. palatinae minores
		A. canalis pterygoidei	
		A. sphenopalatina	

Felis domestica

Vessels marked with a dagger (†) have no homologues in man.

A. carotis communis	A. thyreoidea superior	
	A. carotis interna [vestigial posterior section only; ophthalmic from circle of Willis]	
	A. pharyngea asc.	{ Rr. pharyngei R. palatinus Rr. eustachii A. carotis interna [middle and anterior sections]
	A. occipitalis....	{ †R. accompanying N. caroticus internus Rr. musculares R. cleidomastoideus A. meningea posterior A. tympanica inferior Rr. occipitales
	R. sternomastoideus	
	A. lingualis	
	A. maxillaris externa	
	A. auricularis posterior	
	A. temporalis superficialis	
	A. carotis externa..	{ A. auricularis profunda A. alveolaris inferior A. masseterica.. { R. massetericus R. temporalis prof. post. A. tympanica anterior †A. anastomotica A. meningea media Rr. pterygoidei
	A. maxillaris interna.....	{ A. ciliaris A. centralis retinae A. lacrimalis Aa. palpebrales lat. Aa. temporales prof. ant. †A. zygomatica Rr. musculares A. supraorbitalis A. ethmoidalis externa [=ant.+post. of man] A. meningea anterior A. frontalis †A. ethmoidalis interna
		{ A. buccinatoria A. palatina post. [=minor] †R. gland. orbitalis
	A. infraorbitalis.	{ A. alveolaris sup. post. †A. alveolaris sup. med. A. angularis Aa. palpebrales med. Aa. alveolares sup. ant. Rr. nasales
		{ A. canalis pterygoidei A. palatina descendens.... A. palatina ant. [=major]
	A. sphenopalatina	

mammals, and hence requires no further comment. The branch to the orbital gland (p. 27) is either absent entirely in man, or is so inconsequential that it is not mentioned in text-books. This obviously is correlated with the vestigial nature of the orbital gland in man.

On the other hand, the caroticotympanic artery of human anatomy is not represented in the cat. That this is a secondary specialization in the cat is shown by the fact that a typical caroticotympanic is present in other carnivores (e.g. *Ursus*).

Felis COMPARED WITH OTHER CARNIVORES

Having established the identity of the individual elements of the carotid circulation in the cat, we may now attempt to determine the alterations to which the basic carnivore pattern has been subjected in this animal. Tandler dissected the arteries of the head in twelve species of Carnivora. His series, which represents a fair cross section of the order, has been supplemented and extended by numerous partial and several complete dissections made by us. On the basis of these data the main outlines of the primitive carnivore circulation, and at least the major morphological trends that it exhibits in this group, can be sketched with certainty. Those important to an understanding of the specializations found in the cat may be considered categorically.

(1) *The internal carotid is always smaller than the external carotid.* This is probably a very general primitive condition among mammals, and hence would be of no interest here were it not for the fact that very definite trends can be traced among the Carnivora. The artery is well developed in the arctoids (dogs, raccoons, pandas, and bears), where its caliber is about half that of the external carotid. It is also well developed in the Mustelidae. In *Viverra zibetha* among the civets, Tandler described the internal carotid as "considerably weaker" than the external carotid, and it was a relatively slender vessel (about equal to the ascending pharyngeal) in our specimen of *Nandinia*. Finally, in the hyenas and cats the internal carotid is essentially a non-functional vestige. Thus the internal carotid of the ailuroid carnivores appears to present a picture of progressive degeneration, which reaches its final stage in the domestic cat.

(2) *An anastomotic ramus, passing into the cranial cavity through the orbital fissure, connects the internal maxillary artery with the internal carotid.* This is a simple straight vessel of fair caliber in the raccoons and mustelids (it was absent on both sides of the head

in a specimen of *Mustela putorius*). In the dogs it forms one or more sharp kinks along its course. In *Viverra* and *Nandinia* it exhibits a simple but definite retiform structure in its intracranial part, while the hyenas and cats present the enormous rete already described, which involves not only both the intracranial and extracranial parts of the anastomotic ramus, but also a section of the internal maxillary. On the other hand, the anastomotic vessel is absent entirely in the bears and the giant panda (*Ailuropoda*), and these animals therefore represent an opposite trend.

This anastomotic vessel does not appear to be of general occurrence among mammals, since Tandler apparently found it only in a few rodents outside the Carnivora. It probably originally evolved, for reasons unknown, by simple hypertrophy of the nutrient twigs supplying the cranial nerves that exit through the orbital fissure, since these vessels arise from both the circle of Willis and the internal maxillary, and thus would furnish a connection between these two circulations via interanastomosis of their fine terminal twigs. In the Carnivora the anastomotic vessel then presents two opposite evolutionary trends: in the direction of complete suppression in the Arctoidea, and toward extraordinary elaboration in the Aeluroidea. It is noteworthy that the caliber and complexity of this vessel vary inversely with degeneration of the internal carotid.

(3) *An anastomosis passing across the dorsal surface of the semilunar ganglion connects the anastomotic ramus (2) with the middle meningeal.* This is a thread-like vessel in *Bassariscus* and *Procyon*. It is almost as large as the trunk of the middle meningeal in the Viverridae (*Nandinia*). In *Felis domestica* it exceeds the middle meningeal in caliber, so that the meningeal appears to arise from the anastomotic vessel; in this final condition the anastomosis assumes the form of a vessel connecting the internal maxillary with the internal carotid circulation via the foramen ovale. It thus has the same function in the cat as does the anastomotic ramus described under (2), namely, diversion of blood from the internal maxillary to the impoverished internal carotid circulation; and is another instance of the remodeling of an arrangement existing in primitive carnivores to a new and wholly different end.

The anastomosis was entirely absent in the bear and giant panda, so that these animals again exhibit an opposite trend from the remaining Carnivora.

(4) *An anastomotic vessel, passing through the foramen lacerum medium, connects the ascending pharyngeal artery with the internal*

carotid. This anastomosis has not been noted heretofore, and we have checked it only on *Canis*, *Bassariscus*, *Procyon*, *Ailuropoda*, *Ursus* [*Euarctos*], *Mustela*, and *Nandinia* in addition to *Felis* and *Panthera*. In all these animals except *Felis domestica* the anastomotic vessel is a relatively minor terminal twig of the ascending pharyngeal, the bulk of the ascending pharyngeal supplying pharyngeal structures in the usual way. In the domestic cat, on the other hand, the anastomotic twig is hypertrophied to such an extent that the pharyngeal branches are minor accessory twigs by comparison. In the cat the main trunk continues via the foramen lacerum medium to the circle of Willis; the intracranial part of this vessel obviously represents the distal end of the internal carotid, but the line of demarcation between ascending pharyngeal and internal carotid is no longer determinable in the cat. This, like the specializations considered under (2) and (3), is obviously an arrangement for diverting blood into the internal carotid circulation in the cat. It is surprising that the larger cats (*Panthera*) show no suggestion of the hypertrophy found in *Felis*.

The bears and giant panda again exhibit an entirely different direction of morphological evolution. In them the foramen lacerum medium either is covered with fibrous tissue or is often obliterated entirely. In our black bear a small vessel, probably representing a vestige of the anastomotic artery, ran from the ascending pharyngeal through this tissue; our giant panda had the foramen entirely obliterated, and appeared to lack any vestige of the anastomotic artery.

(5) A "pharyngeotympanic" branch of the ascending pharyngeal artery enters the middle ear via the eustachian semicanal, anastomosing with the caroticotympanic on the promontorium. This vessel, which apparently is homologous with the unnamed tympanic twig of the Vidian artery of human anatomy, is one of the main vessels supplying the middle ear in many carnivores. It was present in all arctoid carnivores examined, and invariably considerably exceeded the caroticotympanic (which ramifies to the same region) in caliber. In the civets and cats, on the other hand, both the caroticotympanic and "pharyngeotympanic" circulations are considerably altered. There is no vessel in *Nandinia*, *Panthera*, or *Felis* that can be certainly homologized with the caroticotympanic artery, and in *Nandinia* and *Felis* there is nothing corresponding to the pharyngeotympanic. In *Panthera* several minute twigs arise from the ascending pharyngeal and pass through the eustachian semicanal

onto the promontorium; these resemble the pharyngeotympanic artery of other carnivores.

Thus it appears that in the Carnivora the posterior parts of the external and internal carotid circulations, from the bifurcation of the common carotid forward to the orbital fissure, form potentially collateral circulations. Because of the anastomotic vessel that inter-connects them via the orbital fissure, either vessel could take over the terminal part of the other with a resulting reciprocal variation in the caliber of the trunks of the two vessels. In the cat this reciprocal variation has been carried to one extreme, with the internal carotid vestigial and non-functional and the external carotid correspondingly increased in caliber. The reverse of this, the internal carotid assuming complete dominance at the expense of the external carotid, probably could not reach a correspondingly extreme stage because of the important vessels arising from the posterior part of the external carotid.

The cervical and petrosal parts of the internal carotid and the ascending pharyngeal artery, because of the anastomotic twig that inter-connects them at the foramen lacerum medium, also form a pair of collateral trunks similar to the external-internal carotid pair. Reciprocal variation between these two trunks is also theoretically possible in either direction, with the condition in the cat representing one of the two possible extremes.

Thus the basic alterations in the carotid circulation of the cat are all designed to divert blood from the external carotid (extra-cranial in position) to the brain. From the functional standpoint there are two possible causes: suppression of the internal carotid *demanding* that blood be supplied to the brain from some other source, and the external carotid was the only other possible source; or establishment of the collateral blood supply to the brain *permitted* degeneration of the internal carotid.

CAUSES FOR THE CAROTID SPECIALIZATIONS IN *Felis*

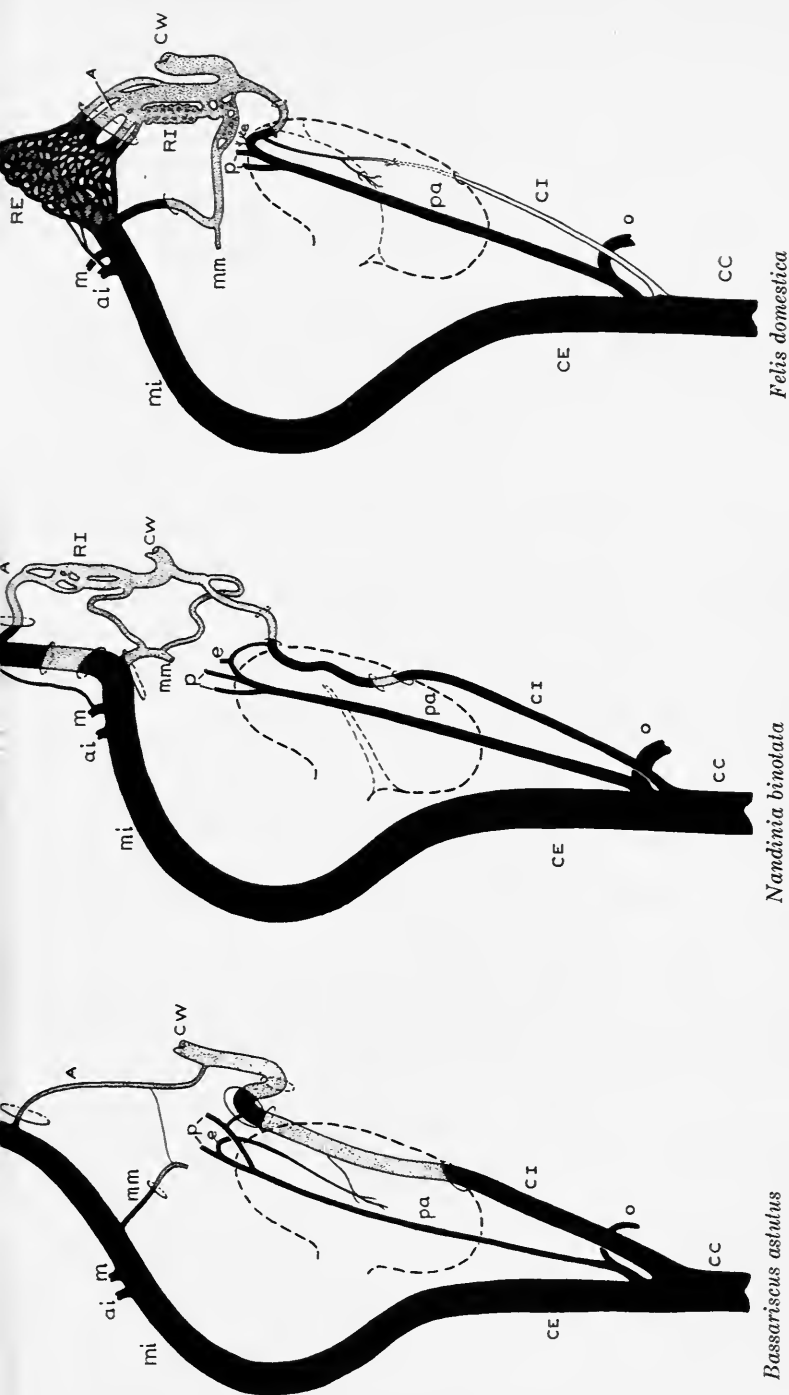
Naturally there is a strong temptation to speculate as to causes for the extraordinary specializations found in the cat. Tandler examined several possible explanations, such as a mechanical obstacle resulting from inflation of the bulla, or that large vessels supplying a powerful facial region may have taken over the blood supply to the brain as a mechanical advantage, but he dismissed them as untenable for what he regarded as "obvious reasons."

The cats are by no means unique in the suppression of the internal carotid. This vessel is also known to be vestigial in many artiodactyls and in *Cavia* among the rodents, and it is of further interest that in these animals a rete mirabile, similar to that found in the cat, is situated between the internal maxillary and the circle of Willis. This appears to be more confusing than helpful in explaining the condition, however. The artiodactyls, the acme of herbivorous specialization, represent almost the ideal functional antithesis of the cats, which exhibit the highest degree of carnivorous specialization among living mammals.

Tandler (1906) studied the ontogeny of the corresponding rete mirabile in the pig. He was able to establish definitely that it does not represent a retention of the primary embryonic vessel network, as had been suggested, but arises later from the internal carotid itself after that artery is well developed, and therefore is a "secondary" formation. This, of course, is an important point from the functional standpoint, since it indicates that the rete is produced wholly by some unknown hydrodynamic factor arising within the parent vessel and not by influences exerted from outside the vessel. We have seen also that the internal carotid functions almost until birth in the cat, not reaching a condition of complete degeneration until immediately before or after birth.

We have seen, furthermore, that the condition of the carotid circulation in the cats merely represents the end-stage of a trend in the Carnivora, and that conditions in certain other carnivore families represent morphologically intermediate stages. A large carotid canal is present in the relatively primitive Oligocene felid *Dinictis*. These facts show that the specialization did not arise suddenly and *de novo* in the cats, and hence that it is probably to be regarded as a mechanical *advantage* rather than a mechanical *necessity*. The parallel between the postulated history of this region in the phylogeny of the cats and its ontogenetic history is almost complete.

Of greatest interest, however, is the fact that the starting points for all the felid specializations are present in the most unspecialized carnivore pattern (fig. 9). In other words, the new pathways that characterize the cat are merely the culmination of a basic trend common to all carnivores except the secondarily specialized bears and giant panda. Thus the cause for the carotid specialization in *Felis* probably should not be sought in the cats themselves (where Tandler was seeking it), but in those carnivores that exhibit the *beginnings* of the specialization (e.g. *Bassariscus*). The same hydrodynamic



Bassariscus astutus

Nandinia binolata

Felis domestica

FIG. 9. Diagram to show the transition from the carotid circulation of a primitive carnivore (*Bassariscus*) to that of *Felis domestica*. The intermediate position occupied by the viverrid *Nandinia* is obvious. Stippled parts are intracranial or run through canals; the outline of the bulla is indicated in broken lines. A, A. alveolaris inferior; ai, A. alveolaris superior; CE, A. carotis communis; CI, A. carotis interna; CW, Circulus arteriosus Willisii; e, R. eustachii; m, A. masseterica; na, A. maxillaris interna; mm, A. meningea media; o, A. occipitalis; p, R. pharyngei; pa, A. pharyngea ascendens; RE, Rete externum; RI, Rete internum.

or mechanical factors that led to the definitive condition in the cat must have been responsible for the first step taken by the carnivores in this direction. The spectacular rete development seen in the hyenas and cats is certainly entirely secondary, and its significance represents a separate problem.

In the present state of our knowledge we cannot answer the question as to why the carotid circulation of the carnivores evolved in the direction it did.

SUMMARY

(1) The carotid circulation of the domestic cat is extraordinarily specialized, even in comparison with most other carnivores. Nevertheless it can be homologized, almost without exception, with the named ramifications of the carotid circulation of man.

(a) Differences between man and the domestic cat involve chiefly a reshuffling of major trunks, on the one hand, and differences in their relative calibers on the other. The terminal branches are usually involved to a lesser extent or not at all.

(b) This suggests that, within the Mammalia, interanastomoses between the terminal twigs of two or more trunks may be the most constant features of a given vessel pattern. Thus the undue attention that has been devoted to the more conspicuous but more variable main trunks has probably contributed to the reputation for erratic variability that has impeded comparative angiology.

(2) All existing descriptions of the carotid circulation of the cat, except Tandler's, contain numerous gross errors. Tandler's description, *because it is part of a comparative study*, is accurate as far as it goes, although it is very incomplete.

(3) From the functional standpoint the most conspicuous features are the suppression of the internal carotid and the far-reaching readjustments that have resulted.

(a) The internal carotid proper is vestigial, its proximal part reduced to an imperforate connective tissue strand.

(1) the section through the carotid canal is completely vestigial and non-functional

(2) the section in the lateral chamber of the bulla has reversed its direction of flow—blood flows posteriorly, from the ascending pharyngeal, to supply the promontorium

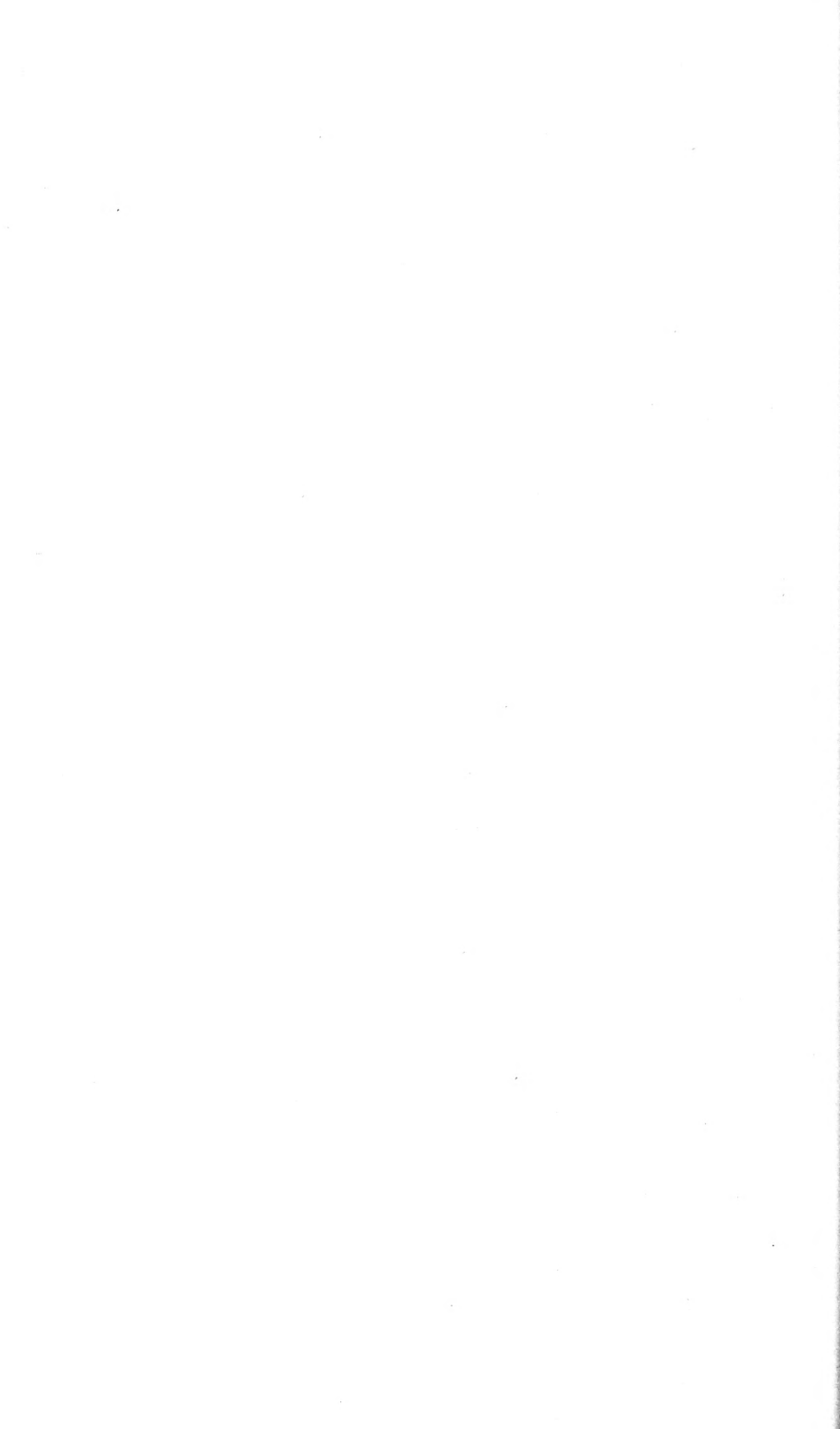
- (3) the section anterior to the foramen lacerum medium has been entirely taken over by the ascending pharyngeal.
- (b) The brain, normally supplied almost entirely by the internal carotid, receives its blood from the external carotid via three novel vessels:
 - (1) an enormous anastomotic vessel connecting the internal maxillary with the circle of Willis via the orbital fissure
 - (2) an anastomotic vessel connecting the internal maxillary with the circle of Willis via the foramen ovale (part of the original middle meningeal artery)
 - (3) the trunk of the ascending pharyngeal having completely taken over the distal part of internal carotid, with its pharyngeal ramifications of very secondary importance.
- (c) There are two retia mirabilia in connection with the anastomotic vessel through the orbital fissure; these are secondary developments, and are probably of secondary hydrodynamic importance:
 - (1) an extensive extra-cranial rete surrounding the internal maxillary at the origin of the anastomotic vessel; the structure of this rete differs radically from any hitherto known from mammals
 - (2) a smaller intra-cranial rete associated with the anastomotic vessel in the sinus cavernosus.
- (d) The internal ethmoidal artery arises extra-cranially, from the internal maxillary, instead of from the circle of Willis as in the Arctoidea. The condition in the Hyaenidae and Viverridae is unknown.
- (e) The orbital artery of other carnivores is represented in the cat by seven independent trunks, apparently a secondary result of the formation of the external rete.
- (f) The ophthalmic artery, when present, arises from the anterior part of the circle of Willis. It was absent in 50 per cent (six out of twelve) of the cases.
- (g) The internal carotid degenerates very late in ontogeny (near parturition).
- (4) All the important adaptations found in the domestic cat are present in some form in all carnivores except the bears and giant

panda; the latter appear to exhibit an entirely different morphological trend.

- (a) The three anastomoses listed under 3b are present in *Bassariscus* in the form of thread-like vessels. These vessels presumably arose from nutrient twigs to surrounding structures, and are not known to occur in non-carnivores.
 - (b) In the Viverridae the caliber of the internal carotid is much reduced, and the caliber of the three anastomotic vessels is increased proportionately. There are also incipient retia mirabilia. Thus the condition in the Viverridae is almost exactly intermediate between the primitive pattern of *Bassariscus* and the highly specialized pattern of *Felis domestica*.
 - (c) The large cats (*Panthera*) resemble *Felis* closely, but are slightly less extreme: the minute internal carotid is often (usually?) perforate, and the distal end of the ascending pharyngeal resembles that of non-felid carnivores.
 - (d) The pattern of the Hyaenidae is known only from Tandler's incomplete description, but as far as known agrees with that of the Felidae.
- (5) Thus the Carnivora may be arranged in a closely graded series leading from the least aberrant pattern (*Bassariscus*), which differs little from that of other mammals, to the extremely specialized pattern of *Felis domestica*. The transition thus exhibited agrees closely with the changes that take place in the pattern during ontogeny in *Felis*.
- (6) Therefore the cause for the carotid specialization in *Felis* is probably to be sought in such a form as *Bassariscus*, rather than in the highly specialized *Felis* itself.

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